A STUDY OF GROWTH, RECRUITMENT AND DISTRIBUTION OF PROTOTHACA STAMINEA IN GALENA BAY, PRINCE WILLIAM SOUND, ALASKA

APPROVED:

.Chairman

Department Head

APPROVED: Fullezich C. Dean Date /.- 11%.

Dean of the College of Biological Sciences and Renewable Resources

Vice President for Research and Advanced Study

BIO_MEDITO: 27 \$E., 31.01.1 <u>.ska</u>

A STUDY OF GROWTH, RECRUITMENT AND DISTRIBUTION OF <u>PROTOTHACA STAMINEA</u> IN GALENA BAY, PRINCE WILLIAM SOUND, ALASKA

A THESIS

Presented to the Faculty of the University of Alaska in Partial Fulfillment of the Requirements for the Degree of MASTER OF SCIENCE

> By A. J. Paul, B.S. Fairbanks, Alaska

> > May 1070

ABSTRACT

Specimens of <u>Protothaca staminea</u> (Conrad), the littleneck clam, were collected by transecting three beaches in Galena Bay, Prince William Sound, Alaska, during the summer months of 1971 for a study of recruitment, growth and distribution.

The average size of <u>Protothaca</u> in Galena Bay at the end of the first growing season is approximately 2 mm in length. At any age, Galena Bay littlenecks are smaller than those from British Columbia. In Galena Bay, eight years are needed for <u>P. staminea</u> to reach a length of 30 mm as compared to three years for individuals from British Columbia.

In Galena Bay, the intertidal distribution of <u>P. staminea</u> generally follows a bell-shaped curve with upper and lower extremes occurring between the tidal heights of +0.73 and -0.76 meters. Youngof-the-year are essentially epifaunal, and the majority of the specimens of all age classes are found within 4 cm of the sediment surface.

The number of individuals surviving annual recruitment into the populations studied was variable.

iii

ACKNOWLEDGMENTS

I wish to thank Dr. Howard Feder for aid and advice in all phases of this study, and for help and guidance in my graduate studies.

I would also like to thank the members of my supervisory committee: Professors R. T. Cooney, Jon Lindsay and Richard Allison for suggestions and constructive criticisms on this thesis.

I would also like to thank Rosemary Hobson (Institute of Marine Science, University of Alaska) for invaluable advice on computer programming techniques; Shirley Wilson (Institute of Marine Science, University of Alaska) for drafting all the figures; Richard B. Nickerson (Alaska Department of Fish and Game) for discussions and for use of an Alaska Department of Fish and Game boat; Carol Anderson, George Perkins, David Roseneau, and Frederick Smith for technical assistance.

TABLE OF CONTENTS

•

-

																														P	<u>AGE</u>
ABST	RAC	Τ.	٠	٠	٠	٠	٠	٠	•	•	•	•	•	٠	•	•	•	٠	٠	•	•	•	٠	•	•	٠	•	•	٠	•	iii
ACKN	OWL	EDO	GME	ENT	ſS	•	•	•	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	٠	•	٠	٠	•	٠	•	•	iv
INTR	ODU	СТІ	[0]	۱.	•	•	٠	•	•	•	•	٠	•	•	•	•	•	•	•	•	٠	•	٠	•	•	٠	•	•	•	٠	1
METH	0DS	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	3
RESU	LTS	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	٠	•	•	•	11
	AG	INC	3.	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	•	•	•	•	•	11
	GR	0\/1	TH I	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	٠	19
	RE	CRI	JIJ	r!1e	ENT	F /	/N[) [DIS	STF	RIE	301	[]	DN	•	•	•	•	•	•	٠	•	•	•	•	•	•	•	•	•	3 5
DISC	USS	101	1.	٠	•	٠	•	•	•	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	48
	AG	INC	.	•	•	٠	٠	•	•	٠	٠	٠	•	•	٠	٠	•	•	٠	•	•	٠	٠	٠	٠	٠	•	*	٠	•	48
	GR	01/1	ΓH	٠	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	50
	RE	CRI	٦II	ГME	ENT	[/	١NE			STR	RIE	307	ΓΙ(ЛC	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	53
FUTU	RE	STI	IDI	[ES	5.	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	64
REFE	REN	CES	5.	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	65

.

L	[S	Т	0F	FI	GU	IR	ES
---	----	---	----	----	----	----	----

FIG	URI																														<u>P</u> /	AGE
1	٠	٠	•	•	•	•	٠	٠	•	•	•	•	•	•	•	•	٠	•	•	•	•	•	•	٠	٠	٠	•	•	•	•	•	4
2	٠	•	•	•	•		•	٠	٠	•	•	٠	٠	٠	٠	٠	٠	•	٠	•	٠	•	٠	٠	•	•	•	٠	•	٠	٠	12
3	٠	٠	•	•	•	•	٠	•	•	•	•	•	•	•	•	•	٠	•	•	•	٠	٠	•	•	•	•	٠	•	•	•	•	15
4	•	•	•	٠	٠	•	•	•	•	•	•	٠	•	•	•	٠	•	•	٠	•	٠	•	•	•	•	٠	•	•	•	•	٠	17
5	٠	•	•	•	•	•	٠	•	٠	•	•	٠	•	•	٠	•	•	•	•	•	٠	٠	٠	•	•	•	•	•	•	•	•	22
6	•	•	٠	•	٠	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	٠	2 8
7	•	•	•	•	•	٠	•	•	٠	•	•	•	•	٠	•	•	•	•	٠	•	•	•	•	٠	•	•	•	•	•	•	•	30
8	•	•	•	•	•	•	•		٠	•	•	•	•	•		•	•	•	٠	•	٠	•	٠	•	•	•	٠	•	•	•	•	33
9	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	٠	٠	•	•	٠	•	•	•	•	•	37
10	•	•	٠	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	٠	3 9
11	•	•	•	•	•	•	•	٠	٠	•	•	٠	•	•	•	٠	•	•	•	•	•	•	٠	•	•	٠	•	•	•	٠	•	41
12	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	٠	43
13	•	•	٠	•	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	٠	•	•	•	•	•	45
14	•	•	٠	•	•	٠	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	•	56
15	•	٠	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	٠	•	•	•	•	•	•	•	•	•	•	•	58
16					•	•					•			•				•	•	•		•	•			•		•		•	•	60

,

LISI UF IADLE	:১
---------------	----

•

_

TABLE																													<u>P</u>	AGE
Ι	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	6
II	•	•	٠	•	٠	٠	•	٠	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	•	e	•	•	•	٠	7
III .	•	•	•	•	•	•	٠	•	•	•	•	•	٠	٠	٠	•	•	٠	٠	٠	•	•	•	•	•	•	•	•	•	14
IV	•	•	•	•	•	•	•	•	•	٠	٠	٠	٠	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	٠	•	20
۷	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	21
VI	•	•	•	•	•	•	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	•	•	24
VII .	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	•	٠	•	•	•	•	•	25
VIII.	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	•	•	•	•	•	•	•	•	•	26
IX	•	•	•	•	•	•	•	•	•	•	•	•	•	٠	•	•	•	•	•	•	•	٠	•	•	•	•	•	•	•	27
х	•	٠	•	•	•	•		•	•		•	•	•			•	•	•	•	•	•	•	•	•	•	•	•	•	•	47

INTRODUCTION

<u>Protothaca staminea</u> (Conrad), commonly called the littleneck clam. is frequently encountered on beaches in Prince William Sound, Alaska (Hubbard, 1971). <u>Protothaca</u> is a species of commercial importance in the state of Washington, and was commercially harvested in Southeastern Alaska until closure of all Alaskan beaches in 1946 due to paralytic shellfish poisoning (P.S.P.). Feder and Paul (unpublished) and R. Nickerson (personal communication) have suggested that a small clam fishery is feasible in Prince William Sound since P.S.P. does not seem to be a problem and many beaches with sizable populations of <u>Protothaca</u> and <u>Saxidomus gigantea</u> (the butter clam) occur in the area.

Considering the extensive distribution of the littleneck clam along the Pacific coast of North America, few papers on the basic biology of the species are available. The most extensive paper is that of Fraser and Smith (1928) which provides information on size at age, sex ratios, size at maturity, and time of spawning for <u>Protothaca</u> from beaches near Victoria, British Columbia. Smith (1928) compared the different types of normally available food and the effects of these food types on growth rates of <u>P. staminea</u>. The only paper providing detailed information on reproduction in <u>P. staminea</u> is that of Quayle (1943) for clams of Ladysmith Harbour, British Columbia. General, but brief, reviews of the species are included in Marriage (1954) for Oregon, Fitch (1953) primarily for California, and Amos (1966) for the entire range of the species. Toxocity of P. staminea

is considered by Felsing (1965) and Quayle (1966, 1969). No intensive work on <u>Protothaca</u> from Alaskan waters is available.

The major purpose of my investigation was to study age and growth of <u>P. staminea</u> in Galena Bay, Prince William Sound. The material collected also provided some basic information on recruitment, distribution and abundance of <u>Protothaca</u>. This project was conducted with funds provided by the University of Alaska's Sea Grant Program for a study of shellfishes in Prince William Sound, Alaska (Grant No. 1-36109).

METHODS

The location of this study was Galena Bay, a small embayment in the northeastern portion of Prince William Sound (latitude 60° 58" N, longitude 146° 44' W), 20 miles from the town of Valdez. Three beaches with varying geology and exposure were sampled. All of these beaches were on the north side of Galena Bay, and were completely covered by water at the highest spring tides (Figure 1). The major features of the study sites are summarized in Table 1.

The weather conditions in the study area were, in general, typical of southcentral Alaska with overcast skies and considerable precipitation (Searby, 1968). Summer air temperatures generally ranged from 7.2° C to 10° C. The extreme surface sediment temperature observed during low tide was 32° C, 14° C higher than the surface sea water temperature of the same day. Water temperatures in Galena Bay ranged from 8° to 18.2° C during the summer months of 1971. The U. S. Department of Commerce (1970) recorded mean surface temperatures in the Cordova region as a minimum of 2° C in February and a maximum of 11° C in August.

Sampling was accomplished by transecting; collections along each transect consisted of a series of continuous stations, defined by a 115 x 22 cm dig. The actual position of the transect on each of the three beaches was arbitrarily selected. The first collection made along each transect (Station 1) was positioned 1 meter up the beach

FIGURE 1. Galena Bay, Prince William Sound, Alaska. The study area for the investigation. Scale: 1" = 1.7 miles.



TABLE I. A description of the three study areas in Galena Bay, Prince William Sound. Description of the beach and its biota refers to appearance at low water.

Area	Wave and Wind Exposure	Longshore Currents	Size of Study Area Feet (Meters)	Slope of Study Area	Substratum of Study Area	Freshwater Drainage	Flora and Fauna
Sheil Beach	Most exposed	Obvious	190 x 70 (57.6 x 21.2m)	6°47'	Fine gravel for first few centimeters overlying fine sediment.	Minimal	No Fucus No <u>Mytilus edulis</u> <u>Balanus</u> spp. very sparse
Eater Beach	Well protected	Not Obvious	220 x 100 (66.7 x 30.3m)	6° 3'	Fine gravel intermingled with large rocks scattered over beach; fine sediment closer to sur- face than on Shell Beach.	Typically minimal; strong outwash after per- sistent rains dissects center of beach	Light cover of <u>Fucus</u> Moderate cover of <u>Mytilus</u> <u>Balanus</u> cover over entire beach
Indian Creek Flat	Protected but exposed to occasional rain squalls	Not Obvious	900 x 900 (272.7 x 272.7m)	0°21'	Mixture of gravel and fine sediment.	Located at mouth of a permanently active stream. Flat. Dissected b numerous tributaries	Light cover of <u>Fucus</u> at upper edge. Moderate cover of <u>Mytilus</u> Moderate cover of <u>Balanus</u> y

 $\widehat{}$

STATION NO.	EATER (Trans	BEACH sect 2)	SHELL	BEACH	INDIAN CR	EEK FLAT
	<u>Meters</u>	Feet	Meters	Feet	Meters	Feet
1	+0.73	+2.4	+0.49	+1.6	-0.06	-0.2
2	+0.55	+1.8	+0.34	+1.1	-0.12	-0.4
3	+0.43	+1.4	+0.18	+0.6	-0.18	-0.6
4	+0.27	+0.9	0.0	0.0	-0.24	-0.8
5	+0.15	+0.5	-0.15	-0.5	-0.27	-0.9
6	0.0	0.0	-0.30	-1.0	-0.30	-1.0
7	-0.15	-0.5	-0.49	-1.6	-0.35	-1.1
8	-0.30	-1.0	-	-	-0.36	-1.2
9	-0.43	-1.4	-	-	-0,39	-1.3
10	-0.52	- 1.7	-	-	-0.42	-1.4
11	-0.64	-2.1	-	-	-	-
12	-0.76	-2.5	-		-	-

TABLE II. Transect stations and their tidal heights for study areas in Galena Bay.

Ŧ

from the location of the first <u>Protothaca</u> encountered in a preliminary trench dug directly adjacent to the sampling transect. The number of stations on a transect was dependent on the width and slope of the beach and the tidal range at the time of collection. On the gravel beaches, all stations were sampled; however, on a mudflat a much larger area was involved and collections were made at 5.75 meter intervals along the transect.

Utilizing reference points from a standard tide table (U. S. Department of Commerce, 1971), and a hand level and a stadia rod, tidal heights were determined for the mid-point of each station. Stations with similar numbers of different transects may have different tidal heights; Table 2 compares station number and tidal heights. Prior to transecting, the vertical distribution of <u>Protothaca</u> was determined by removing the sediment in 2 cm layers to a depth of 8 cm from selected plots (36 x 15 cm) along each transect. Samples collected during these vertical distribution studies were returned to the laboratory and examined under a 2X lens for <u>Protothaca</u>. The sediment from these samples was then used for sieve analyses of grainsize distribution (Morgans, 1956).

Since vertical distribution studies indicated that most of the smaller <u>Protothaca</u> (1.5 to 20 mm in length) were located in the upper 2-3 cm of sediment, it was decided to make collections in two steps at each transect station: a surface collection from the upper 2-3 cm of sediment and a deeper sample to a depth of 12 cm. The surface and

deep samples were placed in separate containers and transported to a collection point for washing. Inclement weather and poor tidal exposures occasionally made it necessary to complete a transect over two tidal cycles.

Sea water used for the washing process was furnished by a gasoline operated portable $pump^{1}$. Each surface sample was washed through a series of screens, the smallest mesh being 1.5 x 1.5 mm. All immediately visible clams were collected. The sediment trapped in the finest screen was returned to the laboratory, and examined for small individuals with a 2X lens.

Standard measurements taken on all clams were greatest length and height (width) (see Fraser, 1928). A sensitive balance was not available in the field; thus no weights are available for clams under 20 mm in length. In an older <u>Protothaca</u>, an increase in shell height is often apparent when the increase in shell length is so small that it is difficult to measure. Therefore, shell height is the most sensitive measurement describing the growth of these clams. Length data is included for comparative purposes.

Age was estimated for all clams less than 20 mm in length utilizing the annular method (Weymouth, 1923); all the larger clams from Shell Beach, and one station on Eater Beach and Indian Creek flat, respectively, were aged. For all specimens aged, the distance between annuli was measured along the radial sculpture line that originated at

Homelite Model XL5.

the approximate center of the umbonal region and roughly bisected the ventral margin of the shell.

Data was processed with an IBM 360 computer, and BIOMED programs (Dixon, 1965) BMDOID, BMDO5D, BMDOIV were adapted for this project. In addition, several simple programs were designed to arrange and plot the data. A one-way analysis of variance was used to test the accuracy of the annular aging technique and to compare growth rates for various years.

RESULTS

<u>AGING</u>

Annuli on valves less than 20 mm in length were quite distinct; false checks which superficially resemble annuli, although present, could be readily distinguished from true annuli (Figure 2). For clams greater than 20 mm in length, false checking and shell abrasion made aging more difficult; however, specimens from all these beaches were aged. The oldest clam collected in Galena Bay was determined to be 15 years old, (L = 47.6 mm).

The validity of the annular aging method was examined with a standard one-way analysis of variance, utilizing the individual shell heights within each age class from Shell Beach as a basis for comparison (Snedecor, 1956). The calculated F ratio indicates that, in general, age classes defined by shell heights are statistically distinguishable, $\underline{P} = 0.01$ (Table III). Similar data from Eater Beach supports the integrity of the aging method used in this investigation (Figure 3).

Histograms plotting size and age indicate that age classes form fairly distinct but overlapping groups (Figure 4). As a result, an aging error of one or two years may occur whenever a specimen is assigned an age based on size alone.

FIGURE 2. The use of shell sculpture as a means of aging <u>Protothaca</u> <u>staminea</u>. (a) Photograph of a 5 year old <u>Protothaca</u> illustrating shell sculpture. (b) Graphic illustration of the shell sculpture between two annuli. A = annulus (winter growth). B = radial sculpture line. C = concentric growth line. A^1 = annulus. A to C = increasing distances between concentric growth lines during spring and early summer growth. C to A^1 = decreasing distances between concentric growth lines during late summer and fall growth. 1, 2, 3, 4 and 5 = successive annuli.



TABLE III. Analysis of variance of shell heights for the various annular age classes of <u>Protothaca staminea</u> for Shell Beach, Galena Bay.

Group (Age)	Sample Size (Number)	Mean Shell Heights (mm)	Standard Deviation
0	7	1.84	0.282
1	5	2.68	0.334
2	6	3.35	0.700
3	19	5.63	0.734
4	21	7.54	0.631
5	44	9.71	1.868
6	52	12.86	3.258
7	44	18.63	3.999
8	45	25.70	4.071
9	59	29.06	1.956
10	37	32.59	1.830
11	20	34.74	2.252
12	9	37.68	1.687

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO
BETWEEN GROUPS	393.8755	12	32.8230	449.6116
WITHIN GROUPS	25.9160	355	0.0730	
TOTAL	419.7915	367		

FIGURE 3. Average length and height plotted as a function of age for specimens collected on a 12-station transect on Eater Beach, Galena Bay. Each symbol represents the average length and height for specimens of a given age at a single station.



FIGURE 4. Size distribution of annular age classes of <u>Protothaca</u> <u>staminea</u> from Shell Beach, Galena Bay. Abscissa represents shell height in millimeters.



GROWTH

The littleneck clams in Galena Bay at a given age are smaller than those collected by Fraser (1928) in British Columbia (Tables IV and V). The annual increase in shell height for the various size classes in Galena Bay is typically 1 to 3 mm. As a result, approximately eight years are needed for <u>Protothaca</u> to reach a length of 30 mm, the minimum size harvested in the sport fishery in Prince William Sound (J. Van Hyning and H. Feder, personal communication).

A comparison of growth rates on the three study beaches indicates that the difference in length at age between beaches is less than 2 mm by the end of the fifth year within the age groupings of 0 to 5 years (Figure 5, Table VI). In older clams, the difference in growth rates between individuals on two other beaches is more pronounced. The annual increase in size for individuals 6 to 12 years of age was generally greatest on Shell Beach and by age 12, specimens from this beach were, on the average, 12 mm longer than those from Eater Beach and 9 mm longer than specimens from the Indian Creek Mudflat (Figure 5).

Average cumulative growth as shell height was plotted as a function of age to determine if average annual growth at a given age varies on a yearly basis. The resultant curves with their consecutively declining slopes suggest that the average annual growth rate has been decreasing for the last twelve years (Figure 6, 7, 8). An analysis of variance utilizing shell heights of all the individuals

AGE		LENGTH	HEIGHT
(Years)		(mm)	(mm)
0	Means	2.06	1.84
	Standard Deviations	0.37	0.28
	Ranges	1.60 - 2.60	1.50 - 2.30
1	Means	2.88	2.68
	Standard Deviations	0.40	0.33
	Ranges	2.20 - 3.20	2.10 - 2.90
2	Means	3.78	3.35
	Standard Deviations	0.90	0.70
	Ranges	2.90 - 5.10	2.70 - 4.60
3	Means	6.53	5.93
	Standard Deviations	1.59	0.73
	Ranges	4.40 - 7.30	4.10 - 6.50
4	Means	8.10	7.54
	Standard Deviations	1.97	0.63
	Ranges	7.00 - 9.80	6.60 - 8.90
5	Means	10.95	9.71
	Standard Deviations	2.13	1.87
	Ranges	9.00 - 18.90	7.60 - 16.30
6	Means	14.70	12.86
	Standard Deviations	3.74	3.26
	Ranges	19.90 - 29.30	9.60 - 26.00
7	Means	21.56	18.95
	Standard Deviations	5.04	3.99
	Ranges	14.50 - 37.20	12.50 - 32.60
8	Means	28.84	25.70
	Standard Deviations	4.52	4.07
	Ranges	15.00 - 36.00	12.90 - 30.90
9	Means	32.68	29.06
	Standard Deviations	1.99	1.96
	Ranges	27.80 - 38.50	24.50 - 34.30
10	Means	36.44	32.59
	Standard Deviations	1.89	1.83
	Ranges	32.00 - 39.70	28.90 - 37.30
11	Means	37.19	34.74
	Standard Deviations	8.09	2.25
	Ranges	33.00 - 46.00	29.30 - 37.30
12	Means	42.08	37.68
	Standard Deviations	2.52	1.69
	Ranges	37.80 - 45.50	34.50 - 39.90

TABLE IV. Shell Beach - average size of clams at age.

TABLE V. Length at end of each year in millimeters for clams collected at Victoria, British Columbia (based on Fraser and Smith, 1929).

1	2	3	4	Yea 5	ar 6	7	8	9	10
12.6 12.9 13.0	25.4 23.2 25.7	35.3 33.4 37.0	43.1 39.9 44.0	48.2 44.3 48.0	52.7 46.3	54.6 49.4	55.9 52.3	5 3. 8	
13.9 13.9	25.7 28.2	27.5 38.6	43.6 48.3	48.7	54.1				
15.7 13.2 11.8	27.4 24.8 30.0	37.2 35.3	44.2 42.9	49.0	52.8	55.8			
13.5	25.8	34.9	41.4	46.3	50.0	52.6	55.8	58.9	
12.6	23.6	30.6	36.2	40.9	44.2	47.4	48.7	49.9	
12.2	22.9 25.9	33.5 35.7	41.7 42.9	47.7 48.5	51.8 52.5	55.7	57.8	59.1	
14.0	24.5 34.2	33.6 39.3	38.7 43.2	43.2 47.1	45.9	48.0	49.5	51.3	53.8
13.4	25.2	32.5	38.8	43.6	46.1	50.3	52.6		
12.2	24.5	35.1	42.8	48.9	54.1	57.8	60.7		
13.1	26.3	37.0	45.6	50.6	54.6	57.7	60.3	62.2	63.4
12.4	23.0	31.6	38.3	42.9	46.4	49.0	50.1	53.6	
11.2	25.4	35.4	44.4	51.1	54.3				
11.3	22.1	31.3	37.3	42.1	45.8	48.8			
11.2	22.0	31.3	38.6	43.6	46.8	49.9	51.1		
12./	2/.4	30.0	42.4	4/.2	50.0	52.U			
14.0	20.4	30.0	42.9	4/.0 17 5	52.0 10 7	54.5			
13.3	20.5	40 2	47.3	52.0	57.3	59.5			
13.4	24.7	33.7	40.0	44.7	48.4	0040			
11.1	26.5	36.0	43.4	49.4	52.9	55.7			
13.6	28.4	38.6	45.8	50.9	54.2	57.3	58.7		
14.6	30.8	41.5	48.8	54.1	57.0	59.9			
17.0 12.5	32.7 22.9	44.4 32.6	50.6 40.0	54.9 45.2	49.3	57.0			

FIGURE 5. Cumulative growth, shell length, for clams from Shell and Eater Beaches, and Indian Creek Flats. Plotted points represent mean values. Shell Beach N = 368, Eater Beach N = 554, Indian Creek N = 642.



TABLE IV. Average shell length for the age groups 0 through 5 for <u>Protothaca staminea</u> from Shell Beach, Eater Beach and Indian Creek Mudtlat.

BEACH			AGE IN	YEARS		
	0	1	2	3	4	5
Shell Beach	2.1	2.9	3.7	6.5	8.1	11.0
Eater Beach	2.1	3.1	4.5	6.0	8.1	10.1
Indian Creek Mudflat	2.6	3.8	5.2	7.1	9.2	11.9

TABLE VII. An analysis of variance for differences in shell height at age three for clams from three to seven years old collected on Eater Beach in 1971.

TREATMENT GROUP (Age)	3	4	5	6	7
SAMPLE SIZE	111	85	31	7	15
MEAN (Shell height, mm, at age 3)	5.0387	5.3917	5.5903	5.8143	5.8400
STANDARD DEVIATION	0.6154	0.7605	0.6843	0.8533	0.6988

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO ¹
BETWEEN GROUPS	17.1317	4	4.2829	9.0481
WITHIN GROUPS	115,4982	244	0.4734	
TOTAL	132.6300	248		

¹H₀: No difference between age groups for shell height at 3 years of age rejected at $\underline{P} = 0.10$

TABLE VIII. An analysis of variance for difference in shell height at age four for clams from four to seven years old collected on Eater Beach, 1971.

TREATMENT GROUP (Age)	4	5	6	7
SAMPLE SIZE	84	31	7	15
MEAN (Height, mm, at age 4)	7.0202	7.5323	8.1000	8.3067
STANDARD DEVIATION	0.9293	0.8027	0.7681	1.0457

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO ^I
BETWEEN GROUPS	27.7891	3	9.2630	11.2149
WITHIN GROUPS	109.8521	133	0.8260	
TOTAL	137.6412	136		

¹H₀: No difference between age groups for shell height at 4 years of age rejected at $\underline{P} = 0.10$

TABLE IX. Analysis of variance for differences in shell height at age five for clams from five to seven years old collected on Eater Beach, 1971.

TREATMENT GROUP (Age)	5	6	7
SAMPLE SIZE	30	7	15
MEAN (Height, mm, at 5 years of age)	9 .49 00	10.4286	10.6800
STANDARD DEVIATION	0.7476	0.9552	1.1675

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO ¹
BETWEEN GROUPS	15,9405	2	7.9702	9.5803
WITHIN GROUPS	40.7652	49	0.8319	
TOTAL	56,7057	51		

¹H_o: No difference between age groups for shell height at 5 years of age rejected at <u>P</u> = 0.10

FIGURE 6. Cumulative growth, in shell height (ages 3-12), for clams from Shell Beach, Galena Bay. N = 368.


FIGURE 7. Cumulative growth, in shell height (ages 3-7), for clams from Eater Beach, Galena Bay. N = 212.



used to create the points clustered around the third, fourth and fifth annular averages of 3, 4 and 5 year olds in Figure 7 indicates that these groups are, in general, statistically different (P = 0.10) (Tables VII, VIII, and IX). Figure 8, which represents a series of back calculations to increase in size of two, three and four year old clams during the growing seasons of 1961-1970, provides a graphic display of the points plotted in Figure 7 and subjected to analysis of variance in Tables VII, VIII, and IX. Figure 8 further illustrates the apparent decline in growth of clams for the past ten years. FIGURE 8. Growth between annuli, in shell height, for clams from Shell Beach.



Year of growth

RECRUITMENT AND DISTRIBUTION

The number of recruits entering and surviving entry into a population can vary considerably on a yearly basis. This is clearly indicated in Figure 9 and 10, which plot the number of clams surviving as a function of the year of settlement. On the beaches examined, individuals of the 1966, 1967 and 1968 year classes are considerably more abundant than those of the 1970 or 1971 year classes, even after surviving three to five years of natural mortality. It is also evident that the 1964 year class, which represents the new recruits to the sport fishery, is not very abundant.

A comparison of the total number of young <u>Protothaca</u> found on the Eater Beach transect (352 clams on a 12-station transect, Figure 11) as compared to the number found on the Indian Creek Mudflat (528 clams on a 10-station transect, Figure 12) indicates the density of young littleneck clams per station in the latter area is somewhat higher. On the other hand, in a comparison of the average number of clams 7 years and older per 0.25 m^2 station along these same transects one finds an average of 55 littleneck clams per station on Eater Beach as compared to 25 per station on the mudflat. Therefore, it appears that survival is better on gravel beaches.

Settlement and survival of clams on a beach also appears to be influenced by tidal height. Figures 11 and 12 also provide a general picture of the distribution of <u>P. staminea</u> on the two beaches in Galena Bay by size. Figure 13 illustrates the distribution and frequency of age classes 0^1 through 6 for different tidal heights along one transect on Eater Beach. The areas with the greatest density of young littleneck clams on this transect fell between the tidal heights of -0.30 and -0.64 meters.

The intertidal distribution of <u>Protothaca staminea</u> in Galena Bay is presently similar to that reported for pre-earthquake Kodiak Island (Nybakken, 1969) and pre-earthquake Olsen Bay (Hubbard, 1971), with the upper and lower extremes occurring between the tidal heights of +0.73 and -0.76 meters, respectively. On the three study beaches the maximum density for clams larger than 20 mm in length, primarily individuals 9 to 12 years of age, occurred between the tidal heights of 0.15 and -0.43 meters, while the greatest density for smaller individuals occurred between -0.43 and -0.64 meters (Figures 11 and 12).

The maximum depth in the sediment at which <u>P</u>. <u>staminea</u> was observed in Galena Bay was 9 cm (Table X). Clams of ages 0 through 7 consistently occurred in the upper two centimeters with most individuals of all age groups within 4 cm of the surface. Clams as large as 10 mm in length were often clearly visible between or just under small rocks. There was no apparent difference in vertical distribution of <u>P</u>. <u>staminea</u> on the gravel beaches or the mudflat.

The term 0 age groups refers to those individuals of the settling year class that have undergone only one growing season (five to six months) before forming their first winter annulus. Thus, individuals referred to as one year of age are actually 17 or 18 months old and have lived through two growing seasons.

FIGURE 9. Abundance of clams 0 to 7 years of age on a twelve-station transect from Eater Beach, Galena Bay.



FIGURE 10. Abundance of clams 0 to 7 years of age on a ten-station transect from Indian Creek Mudflat, Galena Bay.



FIGURE 11. The intertidal distribution of <u>Protothaca staminea</u> from one transect on Eater Beach, Galena Bay. Clams less than 20 mm in length are primarily ages 0-7; those larger than 20 mm in length are mainly ages 8-12.



FIGURE 12. The horizontal distribution of <u>Protothaca staminea</u> from one transect on Indian Creek Mudflat, Galena Bay. Clams less than 20 mm in length are primarily ages 0-7; those larger than 20 mm in length are mainly ages 8-12.



FIGURE 13. The horizontal distribution of <u>Protothaca staminea</u>, age groups 0-6, grouped according to tidal height. Specimens were collected on Eater Beach, Galena Bay. Numbers above each plot refer to tidal height.



Age Code

.

TABLE X. Vertical distribution of clams taken from 13 sample plots in Galena Bay, Prince William Sound, on three beaches. Tidal heights of collections from +0.73 m to -0.48 m.

Depth in Sediment	Number of Protothaca staminea	Average Length (mm)	Number of <u>Saxidomus</u> giganteus	Lengths (mm)
Surface - 2 cm	88	14.0	3	43.4 36.2 4.1
2 - 3 cm	88	26.9	ו	48.0
4 - 6 cm	26	35.7	1	36.5
6 - 8 cm	4	40.4	0	
8 - 10 cm	0	0	0	#* #*

DISCUSSION

AGING

Aging by the annular method is a time-consuming process best accomplished with a dissection microscope. The patterns created by the radial sculpture and the concentric growth lines of the valves are invaluable aids for aging <u>Protothaca staminea</u> by the annular method (Figure 2).

During the winter, increase in shell size is negligible, and growth at the shell margin consists of a series of closely spaced concentric lines which form a winter annulus. Spring growth results in a progressively increasing distance between these lines, and as summer progresses the distance between these lines gradually decreases until a new annulus is formed the following winter. True annuli extend from near the umbo anteriorly and merge with the hinge structure posteriorly. False checks may also appear as an aggregation of fine concentric lines; however, such checks generally fail to merge dorsally, and do not fit within the pattern of gradually increasing and decreasing distances between the concentric growth lines mentioned above.

Generally, size-frequency distribution histograms cannot be used to accurately age <u>P. staminea</u> from Galena Bay (Figure 3). The individual difference in yearly growth within age groups, even when taken from a restricted sample plot, results in a considerable overlap in size distribution. Fraser (1928) found a similar disparity in the range of

sizes within annular age groups for <u>P. staminea</u> from British Columbia, and Quayle (1952) working on <u>Venerupis pullastra</u> in Scotland found that length-frequency distributions could not be used to determine age groups for this clam.

<u>GROWTH</u>

In comparison to growth rates reported by Fraser (1928) for <u>Protothaca staminea</u> in British Columbia, clams in Galena Bay grow much more slowly. The average length for <u>P. staminea</u> at the end of its first year in British Columbia is on the order of 12 mm (Fraser, 1928), while in Galena Bay it is approximately 2 mm (Table IV and V). This slow growth in Prince William Sound is probably the result of the lower water temperatures. The adverse effect of low water temperatures on growth rate has been reported for a number of bivalve molluscs including <u>Pinctada martensii</u> (Kobayashi and Watabe, 1959), <u>Crassostrea</u> <u>virginica</u> (Loosanoff, 1958), <u>Mytilus edulis</u> and <u>Mercenaria mercenaria</u> (Pratt and Campbell, 1956).

A screening technique was not used to collect <u>P. staminea</u> in Prince William Sound during 1970; as a result the 0 and 1 age groups were not collected (Feder, personal communication). In subsequent preliminary attempts to age clams from these collections, the second annulus was assumed to represent the size at settlement; thus, two growing seasons were not recorded. Fraser's paper (1928) does not include a "Methods" section, and lack of clarity of his photographs makes it impossible to interpret the figures included. It is possible that Fraser may have likewise missed the younger age groups in collection, and his aging could be negatively biased.

Both Fraser (1928) and Smith (1928) observed that in Canadian waters the most favorable growth occurred on beaches near strong tidal

50

Π

currents, while poor growth was generally observed on beaches at the heads of quiet bays. An examination of older specimens of <u>P. staminea</u> from Galena Bay supports this observation (Feder, personal communication). The cumulative growth curve (shell length) for <u>Protothaca</u> from Shell Beach is a linear expression (Figure 8). This beach, the most exposed study site, is subjected to long-shore currents. Similar cumulative growth plots for Eater Beach and Indian Creek, protected locations with little current or wave action, provide more standard growth curves which become asymptotic at about age 10 (Figure 5).

In comparing cumulative growth curves for clams of various ages on Shell Beach, it appears that, in general, the growth rates for all age classes are in a state of decline (Figure 6 and 7). It is possible that curves representing the 10, 11 and 12 year groups include specimens that belong to older age groups which might contribute to error; however, it is unlikely that this is the case for 3 to 9 year old clams where annuli are fairly distinct (Figure 2).

Figure 8, which is a back calculation to the increase in size of 2, 3 and 4 year olds during the growing seasons of 1961 through 1970, provides a graphic display of the points subjected to analysis of variance (Tables 7, 8 and 9), and further illustrates the apparent annual decline in growth at a given age. A decrease in growth during the growing season of 1964 is especially noticeable in the four year old clams of that season; it was during that year that the Alaska

Earthquake caused an uplift of 2 feet in Galena Bay. At this time no bias in measurement can be detected that might be responsible for the consecutively declining slopes shown in Figure 6 and 7. Also, no oceanographic data is currently available which might indicate physical trends that could explain this apparent decline in growth rates.

As an alternative hypothesis, Smith (1928) proposes that with an increase in density of clams per unit area, the amount of food available to each individual bivalve decreases, ultimately resulting in an overall decrease in growth rates. In Galena Bay the 1966, 1967 and 1968 year classes were relatively strong ones (Figure 9 and 10) and it may be that the high densities created by these three year classes have resulted in increased competition for available food with themselves as well as the following year classes. If food is a limiting factor in determining annual growth, competition in Galena Bay may have reached the point where growth is being retarded in all year classes. The relative year class strengths of age classes older than seven are incompletely known at present.

RECRUITMENT AND DISTRIBUTION

The differences in year-class strength of <u>Protothaca staminea</u> in Galena Bay (Figures 9 and 19) have also been noted for other bivalve species, e.g., <u>Saxidomus gigantea</u> (Fraser and Smith, 1928), <u>Cardium</u> <u>edule</u> (Hancock, 1970), and <u>Venerupis pullastra</u> (Quayle, 1952). There are a number of interrelated factors affecting larval production in bivalve molluscs, but in general the most important ones appear to be the number and physical condition of mature females and the temperature requirements necessary for the liberation of the larvae (Hancock, 1970). Survival of larvae in the plankton and successful settlement are also affected by several environmental parameters, especially temperature, adequate food supply, predation and favorable conditions for settlement (Hancock, 1970; Thorson, 1966). Data on most of these parameters are not presently available for <u>P. staminea</u> in Prince William Sound.

Hancock (1970), working in England, noted that the number of 0-age group cockles (<u>C</u>. <u>edule</u>) appeared to be poorly correlated with abundance of spawning stock. He also observed that poor to moderate settlements followed years of good to exceptional recruitment. If larval production and settlement of <u>P</u>. <u>staminea</u> is affected by year-class densities in a similar manner, it is possible that the strong year classes of 1966, 1967 and 1968 (Figures 9 and 10) are responsible for the moderate to poor recruitment observed in Galena Bay during the following years.

Strong tidal currents may affect the numbers of settling veligers in the intertidal zone (Fraser, 1928). On Shell Beach, the study site with the strongest currents (Table I), the number of clams under five years of age (seven clams per 0.25 m^2) was consistently lower than that found on the Indian Creek Mudflat (23 clams per 0.25 m^2) where the shore was relatively undisturbed by wave action and currents.

In general, most young <u>Protothaca staminea</u> occur in the lower section of their tidal distribution (Figures 11 and 12). This is probably due, in part, to the environmental stresses acting on young clams at the upper, more frequently exposed portions of the beaches. This distribution also may be the results of selective settlement by veliger larvae or hydrographic concentration of larvae in the plankton at time of settlement (Ryther, 1968; Thorson, 1957). The two-foot uplift of land in Galena Bay following the Alaska Earthquake of 1964 (National Research Council, 1971) may have affected settlement and/or survival of clams at the upper limits of their intertidal distribution during that year. The time of the year for settlement of <u>Protothaca</u> veligers in Prince William Sound is not known.

On most beaches and flats of Prince William Sound there are many temporary and permanent streams fed by rain, melting snow and glacier ice. <u>Protothaca</u> is rarely encountered in areas where permanent freshwater streams flow over or percolate through beach sediments at low tide (Feder and Paul, unpublished). Mortality resulting from rainfall on exposed beaches is probably negligible; however, heavy rainfall may affect distribution of <u>Protothaca</u> by altering beach topography, Freshwater runoff after a period of prolonged rainfall is often responsible

for the active transport of beach sediments; in such areas young clams are washed away with these sediments.

Throughout its range P. staminea is found within 15 cm of the sediment surface and occasionally at the surface (Amos, 1966). In Prince William Sound clams 0 through 4 years of age are essentially epifaunal in their distribution while older individuals exist as subsurface dwellers. Siphon length is probably the limiting factor in determining the depth at which various sizes of clams occur. Sieve analysis of sediment from Eater and Shell Beaches indicates that coarse gravel at the beach surface covers medium gravel and finer sediment. It is probable that the substrate on such gravel beaches affords young Protothaca protection from predation, exposure and ice scouring by providing space between the gravel in which the clams can lodge themselves. These spaces, water filled at high tide, provide a haven where young clams can remain below the level of the beach surface at a depth greater than their siphon length and still feed. On the Indian Creek Mudflat, sediment fills the gravel pore spaces (Figure 16), thereby probably forcing the young Protothaca to remain closer to the surface of the mudflat for longer periods of time than if they had settled on a gravel beach. Clams on mudflats, such as Indian Creek, are more vulnerable when young, and this may, in part, explain better survival of clams on gravel beaches.

In Galena Bay few individuals that settle between the tidal heights of -0.43 and -0.76 meters survive beyond their fourth year, despite the fact that it is here that the heaviest concentration of young clams

FIGURE 14. Cumulative frequency curves for sediment samples taken in one centimeter intervals of depth at Eater Beach, Galena Bay.



FIGURE 15. Cumulative frequency curves for sediment samples taken in one centimeter intervals of depth at Shell Beach, Galena Bay.



FIGURE 16. Cumulative frequency curves for sediment samples taken in one centimeter intervals of depth at Indian Creek Mudflat, Galena Bay.



occurs. This situation suggests that some form of selective mortality exists since the environment is habitable. It is probable that predation is responsible for nuch of this mortality since many forms (foraminiferans, turbellarians, nematodes, and harpacticoid copepods) are reported to prey on newly settled clams (Thorson, 1966). Christensen (1970) indicates that the sea star Astropecten irregularis is capable of swallowing and digesting at least 200 newly settled bivalve molluscs, Spisula subtruncata, per day and that this represents an important factor in determination of year-class success. Sea-star predation on young clams is probably also important in Galena Bay where on certain gravel beaches, concentrations of the sea star Pycnopodia helianthoides occur in the regions of heaviest settlement of <u>P. staminea</u>. This sea star moves over the substrate ingesting small epifaunal organisms, inclusive of P. staminea (Feder and Paul, unpublished). Since young littleneck clams are found near the beach surface, between small rocks or barely covered by sediment, for the first four years of their lives, they are vulnerable to this predator for the entire period. A drill, Natica clausa, is also active in the same region as evidenced by the many drilled valves found here, with some of the shells as small as 5 mm in length (Feder and Paul, unpublished).

Larger <u>Protothaca</u> are also preved upon by the sea stars <u>P</u>. <u>helianthoides</u> and <u>Evasterias troschelii</u> (also common on the same gravel beaches as <u>P</u>. <u>helianthoides</u>). Both of these predators actively seek

out the clams in the sediment and excavate for them (Mauzey, <u>et al.</u>, 1968; Feder and Paul, unpublished). Additional potential predators on the larger littlenecks that occur in the area include <u>Cancer magister</u>, <u>C. gracilis</u>, <u>Hemigrapsus oregonensis</u>, and various bottom-feeding fishes such as the greenling <u>Hexagrammos</u> sp. and the tomcod <u>Microgadus</u> <u>proximus</u>; these species all feed on the beaches during high tide (Feder and Paul, unpublished).

Heavy predation by sea stars and other predators as a factor affecting the lower limits of prey distribution is reported for such vulnerable forms as snails, mussels, barnacles, and sand dollars (Birkeland and Chia, 1971; Feder, 1970; Newcombe, 1935; Paine, 1969, 1970).

FUTURE STUDIES

<u>Protothaca staminea</u> undoubtedly represents a potential, although probably limited, fishery resource in Prince William Sound. Since the variable recruitment and slow growth rates observed for Galena Bay appear to apply throughout Prince William Sound, such a fishery would require a large number of beaches with populations of <u>Protothaca</u> that could be harvested on an 8 to 10 year rotational basis (Feder and Paul, 1973 and unpublished).

However, population estimations must be made for this clam throughout Prince William Sound before such a fishery could be initiated. A detailed examination of the reproductive biology is likewise in order.

The large port facility proposed for Valdez by ALYESKA to receive Prudhoe Bay crude oil will undoubtedly cause some degree of oil contamination as a result of normal shipboard operations, ballast treatment and accidental spillages. Therefore, beyond its potential as a commercially harvestable species, <u>Protothaca</u> may have additional value as an indicator of environmental change, since this clam is the only intertidal invertebrate from Prince William Sound whose natural history has been studied in detail. <u>In situ</u> experiments designed to determine the effect of oil pollution of growth rates, recruitment and mortality of <u>P. staminea</u> would be of great value.

REFERENCES

Amos, M. H. 1966. Commerical clams of the North American Pacific Coast, U. S. Dept. Int. Fish and Wildlife Service Bureau Commercial Fish., Circular 237:1-18.

- Arthur, D. R. 1968. The biological problems of littoral pollution by oil and emulsifiers--a summing up. Suppl. to Vol. 2 of Field Studies, Field Studies Council, London: 159-164.
- Birkeland, C. and F. S. Chia 1971. Recruitment risk, growth, age and predation in two populations of sand dollars, <u>Dendraster excentricus</u> (Escholtz). J. Exp. Mar. Biol. Ecol., 6: 265-278.
- Christensen, A. M. 1970. Feeding biology of the sea star <u>Astropecten irregularis</u> Pennant. Ophelia, 8: 1-134.
- Dixon, W. J. 1965. BMD Biomedical computer programs. Health Sciences Computing Facility, Dept. Preventive Medicine and Public Health, School of Medicine, Univ. Calif., Los Angeles. 620 p.
- Feder, H. M.
- 1970. Growth and predation by the ochre sea star, <u>Pisaster</u> <u>ochraceus</u> (Brandt), in Monterey Bay, California. Ophelia, <u>8</u>: 161-185.

Feder, H. M. and A. J. Paul

- 1973. The littleneck clam, <u>Protothaca staminea</u>, of Prince William Sound, Alaska: a potential fishery resource. 23rd Alaska Science Conference. 1 p.
- Felsing, W. A., Jr. 1965. Proceedings of joint sanitation seminar North Pacific clams. Alaska Dept. Health and Welfare; U. S. Dept. Health, Education, Welfare; Public Health Service. Supt. Documents, U. S. Government Printing Office, Washington, D. C. 34 p.
- Fitch, J. E. 1953. Common marine bivalves of California. Calif. Dept. of Fish and Game. Fish Bull. 90: 102 p.
Fraser, C. M. and Smith, G. M.

1928. Notes on the ecology of littleneck clam, <u>Paphia staminea</u> Conrad. Trans. Roy. Soc. Can., Ser. 3, <u>22</u>, Sect. V, 249-269.

Hancock, D. A.

- 1970. The relationship between stock and recruitment in exploited invertebrates. International Council for the Exploration of the Sea. C. M. 1970 Symposium on "Stock and Recruitment" No. 24. 28 p.
- Hubbard, J. D.
 - 1971. Distribution and abundance of intertidal invertebrates at Olsen Bay in Prince William Sound, Alaska, one year after the 1964 earthquake. In: National Res. Council 1971. The great Alaska earthquake of 1964. Biology. Pub. 1603. National Academy of Sciences, Washington, D. C. 287 p.
- Kobayashi, S., and N. Watabe 1959. The Study of Pearls. Gihodo Press, Tokyo. 280 p.
- Loosanoff, V. L. 1958. Some aspects of behavior of oysters at different temperatures. Biol. Bull. 114, 5770.
- Marriage, L. D.
 - 1954. The bay clams of Oregon, their economic importance, relative abundance, and general distribution. Fish Comm. Oregon, Contrib. 20. 47 p.
- Morgans, J. F. C. 1956. Notes on the analysis of shallow-water[substitute.] J. Anim. Ecol., 25: 367-387.

National Research Council

- 1971. The great Alaska earthquake of 1964. Biology, Pub. 1604. National 1604. National Academy of Sciences, Washington, D. C. 287 p.
- Newcombe, C. L. 1935. A study of the community relationships of the sea mussel. Ecology, <u>16</u>: 234-243.

Nybakken, J. W. 1969. Pre-earthquake intertidal ecology of Three Saints Bay, Kodiak Island, Alaska. Biological Papers of the University of Alaska. No. 9: 1-115.

Paine, R. T. 1969.

- 1969. The <u>Pisaster-Tegula</u> interaction: prey patches, predator food preference, and intertidal community structure. Ecology, <u>50</u>: 950-961.
 - 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecology, <u>52</u>: 1096-1106.
- Pratt, D. M. and Campbell, D. A. 1956. Environmental factors affecting growth in <u>Venus</u> (<u>Mercenaria</u>) <u>mercenaria</u>. Limnol. Oceanogr. <u>1</u>, 2-17.
- Quayle, D. B.
 - 1943. Sex, gonad development and seasonal gonad changes in <u>Phaphia staminea</u> conrad. Jour. Fish. Res. Bd. Canada, No. 2, <u>6</u>: 140-151.
 - 1952. The rate of growth of <u>Venerupis</u> <u>pullastra</u> (Montagu) at Millport, Scotland. Proc. Roy. Soc. Edinburgh. Sect. A (Biology). LXIV. Part IV (No. 20): 384-406.
 - 1966. Paralytic shellfish poisoning-safe shellfish. Fish. Res. Bd. Canada, Nanaimo Biol. Station, Circular No. 75: 9 p.
 - 1969. Paralytic shellfish poisoning in British Columbia. Fish. Res. Bd. Canada Bull. 168: 68 p.

Ryther, J. H.

- 1968. Vol. I. The status and potential of aquaculture. Part II. Invertebrate and algae culture. National Technical Information Service, U. S. Dept. Commerce. p. 104.
- Searby, J. W. 1968. Coastal weather and marine data summary for Gulf of Alaska, Cape Spencer westward to Kodiak Island, ESSA Technical Memorandum. EDSTM 8: 30 p.
- Smith, G. M. 1928. Food as a factor in growth rate of some Pacific clams. Trans. Roy. Soc. Can. (3)22, Sect. V., 287-291.

Snedecor, G. W. 1956. Statistical Methods Applied to Experiments in Agriculture and Biology. 5th ed. Iowa State College Press, Ames. 534 p.

Thorson, G. 1957. Bottom communities (sublittoral or shallow shelf), in Treatise on Marine Ecology and Paleoecology, J. S. Hedgpeth, Ed., Geol. Soc. Am. Mem., <u>67</u>: 261-534.

Thorson, G.

1966. Some factors influencing the recruitment and establishment of marine benthic communities. Netherlands J. Sea Res. 3: 267-293.

United States Department of Commerce

- 1970. National Oceanographic and Atmospheric Administration. Surface water temperature and density. Pacific coast, North and South America and Pacific ocean islands. N.O.S. Publication 31-3. Third edition. 88 p.
- United States Department of Commerce
 - 1971. National Oceanographic and Atmospheric Administration. Tidal current tables. Pacific coast of North America and Asia. 254 p.

Weymouth, Frank W.

1923. The life-history and growth of the pismo clam (<u>Tivela</u> stultorum (Mawe)). State of California Fish and Game Commission. Fish Bulletin, No. 7. 120 p.

BRJ-MEDICAL LINDARY UNIVERSITY OF PLASKA